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I 系統・進化におけるヒト化の問題

Hominid Phylogeny As Seen in the Dentition

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This paper will examine to what extent the study of the dentition can help us to elucidate two types of questions regarding hominid phylogeny. The first type has to do with hominid origins, the second with the degree of relationship obtaining between contemporary hominid taxa in early Pleistocene.

I. Dental evidence and hominid origins

1. How far back can we trace the origin of the hominid phylum? The answer to that question depends of course on the way the term 'hominid' is defined. It used to be thought that the hominid grade of evolution could be defined by either one of the following characteristics: erect posture, small canine tooth, and tool making. No problem arose as long as these three features seemed to appear together (v.g. the Australopithecine material found up to the late 50's). Problems began to arise when it became likely that some erect primates did *not* make tools (v.g. *Australopithecus robustus*). These problems were compounded when it appeared that primates with small canines may neither have walked erect nor have been making tools (*Gigantopithecus, Oreopithecus,* possibly also *Ramapithecus*).

In other words, to identify the time of origin of the hominid phylum it is first necessary to answer the question: *is a small canine a sufficient condition to qualify as hominid*?

For a long time it was nearly universally accepted that the hominid type of dentition derived from dentitions with a 'canine complex' as seen in pongids. This conviction was based on both indirect and direct evidence. Overhanging tips of upper and lower canine in perfect occlusion, long roots of the canines in man, large size of the deciduous canine, relative length of P_3 and P_4, and late eruption of the canine made up the indirect evidence. Direct evidence was found in the relatively large size of the canine in Neanderthal Man and *Homo erectus*.

This way of thinking made it easy to identify hominid forms as soon as they appeared, since a small canine was considered to be sufficient evidence. In recent years, however, this view has been questioned on several grounds pertaining to both the indirect and direct evidence mentioned above. Indirect evidence has been shown recently to be much less clear than was commonly believed (Kinzey, 1971).

Direct evidence, which has been accumulating at an accelerating rate during the last ten years, suggests today a different interpretation. It has been established, for instance, that as long as 3.10^6 years ago the mandibular and dental mechanism of *Australopithecus* was about as unlike that of apes as in present-day man. Simons (1969) concludes after reviewing the evidence: "the living habits typical of *Australopithecus* arose long before the late Pliocene." In other words, there is no indication whatever in the fossil record that *Australopithecus* derived from a form with large canines.

The discovery of new specimens of *Ramapithecus* and the restudy of the formerly known material confirm the preceding conclusion. What is now designated as the "Rama-Australopithecus dental complex" (Simons, 1969) comprises, among other traits, very small canines and is known to have been in existence for over 10 million years (perhaps as many as 20). However, and this is most important to note, in spite of the short canine, this complex has been shown (Andrews, 1971) to include several pongid traits. Thus, direct evidence indicates that a short canine is not necessarily associated with an entirely hominidlike dental complex. On the other hand, the finds of forms like *Gigantopithecus* and *Oreopithecus* show that the observation of Andrews holds also for genera other than *Ramapithecus*.

2. The questions raised by the evidence considered above can be formulated as follows: a. it is not enough to show that a form had a short canine in order to establish its hominid status, since undoubted hominids (Australopithecine) are now known to have derived from forms that had already short canines and since forms with short canines appear to have shared also a number of characters with the pongids; b. it may thus become necessary to redefine 'hominid' in a more comprehensive way. Pilbeam (1968) has attempted to include in that definition a number of features covering the entire dentition, including occlusal pattern, mode of implantation of the roots, and disposition of the tooth rows. On the basis of these characteristics he states that it is difficult to tell whether *Ramapithecus* should be classified as a hominid or as a manlike pongid, and he expresses the view that this questionmay well be "a matter of semantics." c. the borderline between hominids and pongids having thus become more and more arbitrary, the time of origin of the hominid phylum is thus likely to be pushed back in time much more than was thought

possible until recently (v.g. L.S.B. Leakey (1967) wants to recognize as hominids some of the East African lower Miocene fossils).

3. If any lesson can be drawn from this first section of our inquiry, it is that teeth are far from being a convenient basis for distinguishing the first appearance of hominids. The latter is perhaps best identified by traces of the new behavior that characterized it, such as learning, cooperation, etc. Dental evidence will be most important where it helps to identify the presence of such types of behavior.

II. Dental evidence and Australopithecine taxonomy

In the original find published by Dart in 1925 the dentition figured already among the features which drew the attention, particularly the shape of the dental arch and the small size of the deciduous canine. Dart's deductions, much discussed at the time, were confirmed by later finds of adult specimens. The Australopithecine dentition may thus be said to have been the first piece of evidence to suggest that *Australopithecus* belonged to the hominid line of evolution, and not to the pongid line (Gregory, 1939). From a methodological point of view it is interesting to note why, in spite of so many hominid characters in the dentition, many experienced anthropologists were so slow in recognizing the phyletic status of *Australopithecus*. As noted by Le Gros Clark (1967), "inadequate and erroneous statistical results" purported to demonstrate no difference in size or shape between some of the fossil teeth and those of modern anthropoid apes.

Today, few anthropologists would hesitate to recognize *Australopithecus'* dentition as that of a hominid. The remaining moot point is whether it can be regarded ancestral to *Homo*. Von Koenigswald (1967) for instance believes the anterior dentition to be too much reduced to be that of an ancestor of *Homo erectus*. Similarly, P_3 is more molarized than in the later hominids from Southeast Asia.

Just as dentition played an important role in the early controversy on the hominid status of the Transvaal finds, so today it forms the major topic of discussion when discussing the relative taxonomic status of the two forms that coexisted in early Pleistocene Africa: *Australopithecus* and *Paranthropus*. Those holding for a generic distinction (Robinson) as well as those believing that the distinction is at most specific (Tobias, Simons, Frisch), both rely heavily on an analysis of the dentition. This by itself would suffice to show that the dentition, taken alone, cannot be expected to yield an adequate criterion for deciding this point of taxonomy. The latter conclusion becomes even more evident when it is realized that the differences observed between *Australopithecus* and *Paranthropus* are much better marked in the dentition than in the cranial capacity or in the locomotor system.

In the last ten years one more find by L.S.B. Leakey has become the object of heated discussion: the fossil hominid christened by him *Homo habilis*. Here again it is the dentition which forms the focal point of the controversy regarding the inclusion of this specimen in the genus *Homo* or *Australopithecus*.

Those who exclude *Homo habilis* from *Australopithecus* stress the relative narrowness of the postcanine teeth, especially in the mandible. The opponents (v.g. Robinson, 1968) point out that such a distinction is possible only because only a very small sample of Australopithecine teeth has been considered. With larger samples, it is argued, *Homo habilis'* teeth are seen to fall mostly toward the upper end of the range of variation at present known in the Australopithecine material and *not outside* this range. Moreover, Robinson shows the length/breadth index used by Leakey et al. to have extremely low phyletic valence so far as hominids are concerned, since this index shows wide overlap in its ranges for *Australopithecus, Paranthropus and Homo erectus*. To this criticism of Leakey's position, Robinson adds an interesting observation: if one bases one's judgement not on the relative narrowness of the postcanine teeth but on the relative size of the lower canine to the anterior lower premolar, the specimen designated as *Homo habilis* is seen to resemble *Australopithecus*, while the latter appears to differ significantly from *Paranthropus*.

The lesson taught by the second part of our inquiry seems thus to be first of all that the full range of variability should always be taken into consideration and that a comparative study should always wait until a sufficient number of specimens are available to make such a range reliably known. It is also sobering to see how, once more, dental evidence can be pulled in so many different directions!

III. Conclusions

The study undertaken in order to answer the question formulated at the beginning of this paper has resulted chiefly in identifying more closely the problems to be faced by the student of the dentition of early hominids. While recognizing the necessity of relying on dental evidence, both because of the nature of the preserved evidence and because of the reliability of many of the features apparent on the dentition, it is important to be clear on the limitations of this evidence, especially of the metric features.

These limitations are seen to result chiefly from the variability characteristic of the hominid—and of the primate—dentition and from the personal coefficient inherent in the techniques of measurement. Ways to make up for these limitations would

be: 1. to obtain a correct estimate of the amount and kind of variability characteristic of living primate species; 2. to refrain from speculations too narrowly based (insufficient number of fossil specimens); 3. to make sure either that all measurements are taken by the same person or that the measuring methods are similar.

A clearer definition of the problems raised by the study of the dentition of early hominids is probably the first step toward solving these problems and at the same time clearing up some of the taxonomic confusion that currently obscures much of the discussion about the origins of man.

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霊長類の系統進化からみた hominization

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はじめに

hominization，すなわちヒト化の成立を考えるに当っては，それを単にその時点における変革の諸要素から考究するのみでなく，広く，その成立前に至るまでの歴史的状況についても，適確な把握を行うことが必要である。ここでは後者の必要性に添って霊長類の系統進化を眺め，hominization 考察の資としたい。もともと，ヒト化の考察に近づく以前に，霊長類に属する諸主幹が，系統進化上，互いにどういう関係にあるかについて，必ずしも一般的見解は定っていない現状である。むしろ，従来の見解を再検討すべきとの意見も，少くないというべきであろう。したがって，論述の内容が，大なり小なり仮定，感想に傾きがちにならざるをえないことを，あらかじめお断りしておく。また，本稿は研究会記録として草されたものであるが，講演内容に若干手を加えてまとめることとした。

生活様式としての樹上性

まず，原猿の段階について考える。出発点に相当するとされるツパイ（類）が，それに近縁な，かつての原始食虫類ともども，現生食虫類一般ほどに執ように，地上・地下性であるとは考えにくい（岩本，1971 を参照）。むしろ，既に，適度に樹上にもすむ習性をもっている。このことが，とりも直さず，大きな特殊化を欠くことと関連している。ツパイ，あるいはツパイ的なものから，長い間にはかなりさまざまな原猿が分化した。他方では，分化の多くが環境の変化の中で，絶えていった。ここで一言つけ加えるならば，それら絶滅が，いわゆる competition のイメージの中にある敗北で律せられるものとは思われない。competition に「おかれなかった」ものが〝適者〟として生活をつづけ，あとの進化の基幹となることすら，ありえぬことではない。

さて，高等霊長類，たとえば旧世界ザルにおける，枝をにぎり，食物をとる手，あるいは新世界ザルにおける，枝をにぎる（？）尾などをもって，樹上性への適応と考えるならば，原猿一般にはそのような特徴は不完全であり，樹上性への適応に徹していないことになる。しかし，現実に原猿が樹上生活者であることは疑いない事実である。しばしば，前述の意味において，原猿は樹上生活に適応してはいても，適応しきってはいないといった感じの表現をみることがあるが，もともと，樹上性といい，地上性といい，単にそれぞれ，そのような生活様式を表現する以上に，身性上の適応内容を表現しうるものとは思われない。

言いかえれば，原猿は原猿なりに樹上に適応しきったものとして，原猿の総体を見てみる必要がある。多くの原猿，あるいは手足の指における平爪の発達は，からだが食虫類大から大化する傾向と，夜行性は昆虫食と，立体視は樹上における昆虫食および鼻口部の退縮と，それぞれ互いに関連をもって，樹上性との矛盾を生じていないとみるべきであり，それら特徴を，ばらばらに分離